Sustainability of Vegetation Communities Grazed by Elk in Rocky Mountain National Park

By

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Abstract. Current management of much of the worlds' grazing lands is either based on changes in plant species composition or on other management evaluation programs that emphasize changes in net aboveground production. Management based solely on changes in aboveground production has been criticized as too limited in view, because it ignores root production, nitrogen pools, nutrient processes, and the long-term sustainability of the ecosystem. The purpose of this study was to compare the effects of elk (*Cervus elaphus*) grazing on aboveground production, internal nitrogen (N) fluxes, N pools and inputs, and elk nutrient transfers across the landscape in different vegetation types in Rocky Mountain National Park (RMNP), Colorado. Nitrogen processes and possibly N pools were significantly reduced in the willow community, but not in the upland grass/shrub community. Nitrogen mineralization rates were lower in grazed versus ungrazed short willow sites ($P = 0.07$; n = 4 sites), as were nitrate (NO_3) pools ($P = 0.10$), but not in tall willow sites ($P > 0.10$; n = 4 sites) after 4 years. There was about half the annual N inputs to the soil surface in grazed willow sites (5.79g $N/m^2/yr$ = annual herbaceous biomass – offtake + litterfall + elk urine and feces) compared to ungrazed sites (9.66 g $N/m^2/yr$ = annual herbaceous biomass + litterfall), suggesting elk herbivory and movement led to a net loss of N in the willow vegetation type. Elk substantially reduced the annual growth of willows (*Salix* spp.) by 98% after 35 years and 66% after 4 years of treatment. Thus, height and canopy size of willows were reduced as well as willow litter biomass (65 $g/m^2/yr$ in ungrazed versus 33 $g/m^2/yr$ in grazed), and N yield of willows was 64% less in grazed plots. Elk grazing had no significant effect on other soil N pools (NH_4) or litter decomposition rates in either of the two willow types, nor on any nitrogen process rates or pools in the upland grass/shrub type ($P > 0.10$). Nitrogen concentrations in plant tissue were not influenced for the most part by elk grazing (increased N concentration found in only 4 of 13 species). Elk apparently also transported N away from aspen at an even higher rate (N inputs were 1.65 g $N/m^2/yr$ in grazed sites vs. 3.79 g $N/m^2/yr$ in ungrazed sites). Elk grazing reduced shrub biomass at 35-year treatments in upland grass/shrub communities, but led to more N inputs to the soil surface in this vegetation type (2.28 g $N/m^2/yr$ grazed versus 0.59 g $N/m^2/yr$ ungrazed). CENTURY modeling supported these observations. This soil N model predicted almost no change (0.5–2% less) in N or carbon (C) pools in 50 years in the upland grass/shrub vegetation type, but greater losses in the willow type. If elk population levels were increased to carrying capacity in the ecosystem (about 25% more consumption) projected losses after 50 years were greater, but still <4% for soil C and 1% for soil N in the upland type, and 6% for soil C and 2% for soil N in the willow type. Total shrub C was projected to decline 10% in 50 years in the willow type at current elk densities. We recommend conservative management of elk numbers and grazing until additional years of measures are gathered on the lower mineralization rates in the short willow type and until the projected declines in N pools can be verified.

Keywords: *Cervus elaphus*, elk, mineralization, nitrogen, overabundance, overgrazing, Rocky Mountain National Park, sustainability, willows.

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Current management of much of the world's grazing lands emphasizes changes in plant species composition (Dyksterhuis 1949; Lauenroth and Laycock 1989). One common example of current grazing management limits for western U.S. rangelands is the "increaser-decreaser-invader species" concept of Sampson (1919). Change in aboveground production of plants (Westoby et al. 1989; McNaughton 1993) is another common criteria for setting grazing limits. Milchunas and Lauenroth (1992) rated the long-term ability of the system to sustain productivity under the level of grazing as the highest priority for rangeland management. Change in net aboveground production due to grazing is also currently used to evaluate and manage many western U.S. rangelands, both in national parks, national wildlife refuges, and other public lands (Milchunas and Lauenroth 1992; Biondini et al. 1998). But emphasizing net aboveground production has been criticized as an incomplete view, in that changes in aboveground production might be short-lived and at the expense of root biomass (Belsky 1986) or long-term N pools and soil organic matter (Risser and Parton 1982; Burke et al. 1989). We selected elk grazing in RMNP, Colorado as a study situation where we could sample and compare both effects of elk on aboveground plant production and also effects of elk herbivory on longer-term ecosystem variables such as belowground root biomass, N pools, N inputs, soil organic matter, and N cycling.

Elk have become increasingly abundant in Rocky Mountain ecosystems in the U.S. and Canada. The elimination of large predators, disruption and loss of migration routes, and the creation of artificial forage sources in towns and developed areas have contributed to possible overconcentrations of elk (Wagner et al. 1995). Density-dependent regulation of elk in national parks has been questioned as to its ability to produce the expected equilibria behavior in animal populations (Ellis and Swift 1989), although net aboveground production has been maintained or even increased under natural regulation (Frank and McNaughton 1992, 1993; Singer et al. 1998a; Huff and Varley 1999). In this study, we explore an alternative approach to evaluating the appropriate numbers of ungulates based on the premise that alterations in ecosystem nutrient pools and flows will alter sustainable plant production and can also drive plant species composition changes.

Nitrogen is an essential nutrient that determines ecosystem production in most temperate ecosystems. Ecosystem N pools may take centuries to accumulate and turnover rates may be slow. In ecosystems with a high availability of N, plant species typically have a higher requirement for N and cycle N more rapidly. Organic matter content of the soil is also closely tied to N availability and ability of the soil to hold moisture. Depletion of N and soil organic matter by ungulates could reduce long-term plant productivity and alter plant species composition since many plants have specific N requirements.

Ungulates may be more than just consumers of plants and products of ecosystems. Ungulates may also be regulators of ecosystem processes (Frank and McNaughton 1992; McNaughton 1993; Hobbs 1996). The indirect effects that ungulates may have on ecosystem processes may exceed their direct effects of consuming plants. These indirect effects may include changes in N and defense chemical concentrations in plants, changes in the quality and quantity of litter, and changes to decomposition and mineralization rates (Fig. 1). Grazing may result in increased N availability to plants by reducing root biomass and thus microbial biomass, which reduces C:N ratios (Schimel et al. 1985; Holland and Detling 1990; Seagle et al. 1992). Ungulate feces and urine provide large inputs of soluble N that is readily available to plants (Risser and Parton 1982; Bazely and Jeffries 1985; McNaughton 1990), and the excretions promote decomposition rates (Seagle et al. 1992; Pastor et al. 1993). Nitrogen is more available to plants on grazed sites (Holland and Detling 1990; Seagle et al. 1992), especially near the soil surface where it is more accessible to plants (Archer and Smeins 1991). As a result, uptake rates of N by plants, plant tissue concentrations of N, N mineralization, and aboveground production of plant biomass may be increased on grazed sites (Moss et al. 1981; McNaughton 1984; Coughenour 1991; Frank and McNaughton 1992; Singer and Harter 1996; Frank and Groffman 1998). Ungulates may preferentially graze on plant regrowth from previously grazed sites leading to improved body condition and higher reproductive success (Moss et al. 1981; Iason et al. 1986; Gordon 1988) in a positive feedback loop that maintains grazing "hot spots" (McNaughton 1988).

Alternatively, ungulate grazing may result in reduced N pools and reduced N mineralization rates (Risser and Parton 1982; McInnes et al. 1992; Ritchie et al. 1998). Ritchie et al. (1998) reported that the resource limiting plant growth might dictate whether ungulates accelerate or decelerate N cycling and plant responses. If the plants are N limited and ungulates select N-rich plants and thus increase the dominance of plants with low tissue N, then litter quality, decomposition, and N
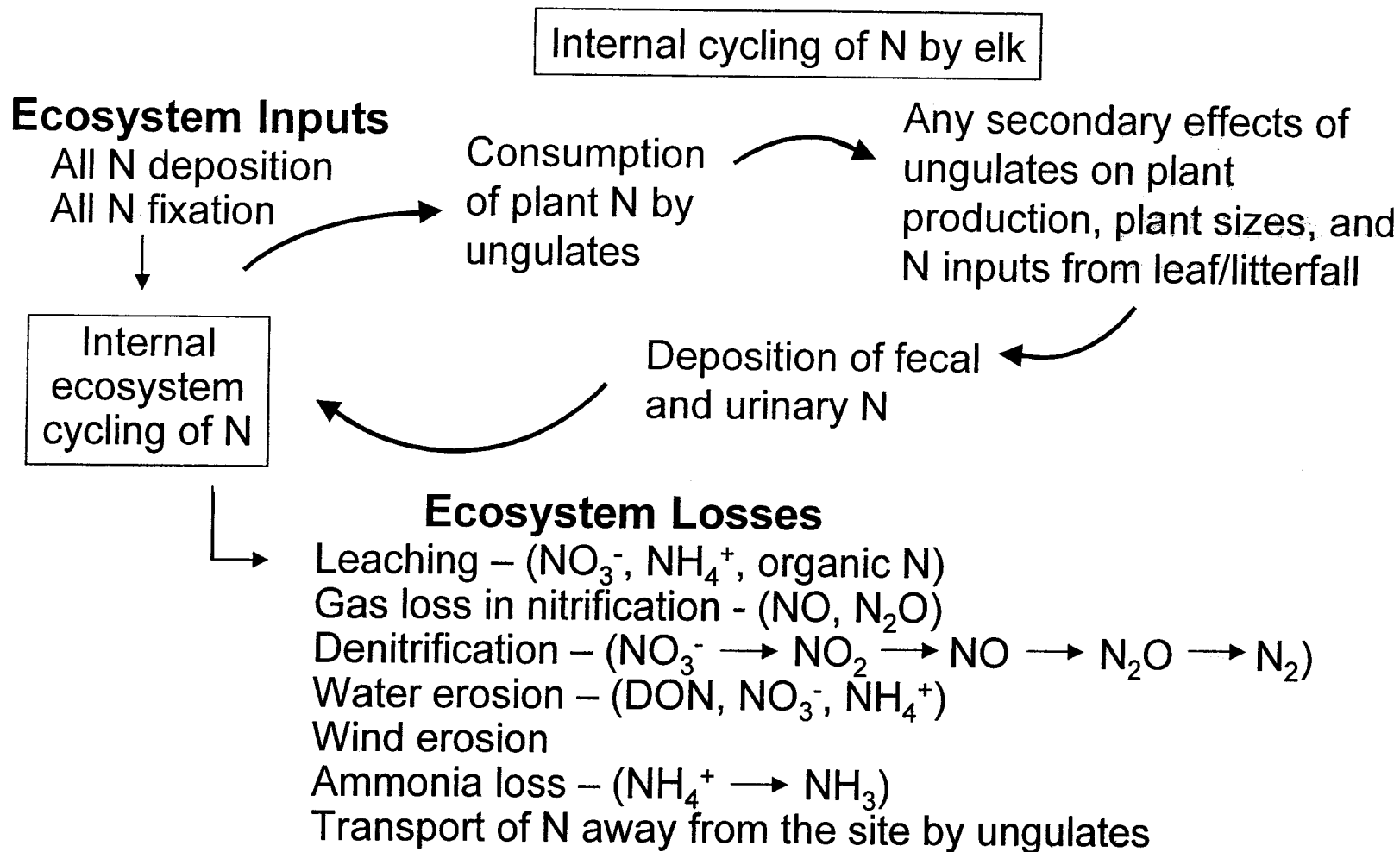
Ecosystem Inputs

All N deposition
All N fixation

Consumption
of plant N by
ungulates

Any secondary effects of
ungulates on plant
production, plant sizes, and
N inputs from leaf/litterfall

Internal
ecosystem
cycling of N

Deposition of fecal
and urinary N

Ecosystem Losses

Leaching – (NO_3^-, NH_4^+, organic N)
Gas loss in nitrification - (NO, N_2O)
Denitrification – ($NO_3^- \rightarrow NO_2 \rightarrow NO \rightarrow N_2O \rightarrow N_2$)
Water erosion – (DON, NO_3^-, NH_4^+)
Wind erosion
Ammonia loss – ($NH_4^+ \rightarrow NH_3$)
Transport of N away from the site by ungulates

Fig. 1. Schematic diagram of N flows and fluxes demonstrating internal cycling of N by elk and ecosystem, or external inputs and outputs. Nitric oxide is represented by NO and DON represents dissolved organic nitrogen.

mineralization is lowered. However, if the dominant plants have high tissue N and/or tolerate herbivory, then herbivory will likely accelerate N cycling.

We conducted this study to determine whether: (1) elk herbivory results in a net gain or net loss of N inputs to the soil surface of the elk winter range; (2) there is a net transfer of N between vegetation types on the winter range or between seasonal ranges; (3) there are any secondary effects of elk on N pools or inputs through structural changes to the plant communities; (4) elk influence ecosystem processes such as mineralization rates or decomposition rates; and (5) there are long-term projections for N losses or N gains due to elk.

Study Area

The elk winter range in RMNP is located in the upper montane zone on the eastern slope of the Continental Divide and includes four major valleys: Beaver Meadows, Horseshoe Park, Moraine Park, and Hallowell Park (Gysel 1959; Stevens 1980; Hobbs et al. 1981; Zeigenfuss et al. 1999). The area is about 10,000 ha in size and ranges from 2,400 to 2,800 m in elevation. Valley bottom vegetation includes sedges (*Carex* spp.), grasses, and riparian shrubs [willow (*Salix* spp.), birch (*Betula* spp.)]. Slopes are vegetated by ponderosa pine (*Pinus ponderosa*)/shrub, mixed conifer (ponderosa pine/ Douglas fir (*Pseudotsuga menziesii*)), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), and upland grass/shrub [predominantly bitterbrush (*Purshia tridentata*)] vegetation types.

35-Year Exclosure Sites

National Park Service staff established three exclosures in Beaver Meadows in 1963. Exclosure 1 (0.4 ha) supports primarily upland grass/shrub type; exclosure 2 (1.2 ha) supports aspen, upland grass/shrub, and willow type; and exclosure 3 (0.4 ha) supports aspen and mesic meadow. The upland grass/shrub type is primarily big sagebrush (*Artemisia tridentata*), with sparse bitterbrush and rabbitbrush (*Chrysothamnus viscidiflorus*). Predominant grasses include junegrass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and mountain muhly (*Muhlenbergia montana*). The willow type supports mountain willow (*Salix monticola*), planeleaf willow (*S. planifolia*), and Geyer willow (*S. geyeriana*). Canadian reed grass (*Calamagrostis canadensis*) and sedges (*Carex* spp.) predominate in the understory, as well as cow parsnip (*Heracleum*

sphondylium), a forb species. Major grasses in the mesic meadow include smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), and timothy (*Phleum pratense*), while the predominant forb is golden banner (*Thermopsis divaricarpa*) (Table 1).

4-Year Exclosure Sites

Sixteen exclosures were established in 1994 on the park's elk winter range in montane riparian and upland shrub communities. These sites were randomly located within strata using GIS procedures. Exclosures prevented large ungulate (deer and elk) herbivory, but did not exclude smaller herbivores. Areas inside the exclosures were considered the "ungrazed" treatment. "Grazed" treatment areas were located adjacent to these exclosures in the same vegetation community types, but beyond the area of any influence of the exclosure fence line (at least 5–7 m distant).

We focused on four of the exclosures that were established in short willow communities, four in tall willow communities, and four in upland grass/shrub communities, which were predominated by bitterbrush (Table 1). Short willow sites make up the largest part of the willow communities in the park (short willows, including dead, saplings, intermediate and low density willows make up 70% of all the willow communities, while tall willows make up the remaining 30%; Peinetti et al., this volume). Willow communities (both short and tall) make up only 4% of the elk winter range, although willows comprise a larger percent (30%) of the core winter range (Singer et al. 1998b) and about 11.7% of elk winter diets (Singer et al., this volume). Elk densities and consumption rates are higher in short willow communities than tall willow communities (30 ± 6 elk/km² vs. 24 ± 10 elk/km²).

Methods

Nitrogen Pools

Aboveground N Pools

Herbaceous standing crop biomass was sampled by clipping three to five randomly placed 0.25-m² circular quadrats at each ungrazed and grazed site at 35-year and 4-year exclosures. All graminoids and forbs within the quadrat were clipped to measure annual peak production. Vegetation was oven dried at 55°C for 48

Table 1. Sampling locations for all ecosystem parameters showing in which treatment and vegetation type they were measured.

| Parameter measured | 4-year exclosures (n = 12) | | 35-year exclosures (n = 3) | | |
	Willow	Upland grass/shrub	Willow	Upland grass/shrub	Aspen
Litterfall	x	-	-	x	x
Herbaceous production	x	x	x	x	x
Shrub production	x	x	x	x	-
Nutrient concentration	x	x	x	x	x
Consumption by elk	x	x	x	x	x
Decomposition	x	-	-	-	-
N mineralization	x	x	x	x	x
Soil N availability	x	-	x	x	x
Soil N concentration	x	-	x	x	x
Root production and N concentration	x	x	x	x	x
Elk feces deposition (grazed plots only)	x	-	-	x	x

hours and then weighed. Visual estimates of percentage bare ground, moss, lichen, cacti, and shrubs were also recorded. Shrub current annual growth (CAG) was sampled from three to five 9.3-m² circular plots at ungrazed and grazed sites following Singer et al. (1994). Regression equations were developed for prediction of willow production for the three major willow species and bitterbrush (Peek 1970). R² values for these equations were high and ranged from 0.75 to 0.92 (Zeigenfuss et al., this volume). Shrub production values for sagebrush were estimated based on average twig weights and average twig counts per plant.

Nutrient concentration (% N) was measured at 35- and 4-year exclosures on composite graminoid and forb samples and shrub CAG twigs in ungrazed and grazed sites in August 1998. Samples were analyzed for concentrations of C, N, lignin, acid detergent fiber (ADF), cellulose, dry matter digestibility, calcium, manganese, magnesium, phosphorus (P), potassium, copper, zinc, and iron. Nutrient analyses were performed at the Range Nutrition Laboratory at Colorado State University, Fort Collins, Colorado.

Belowground N Pools

Total C and N in soil and sand fraction were determined at all 4-year exclosures as described in Menezes et al. (2001). In 35-year exclosures, 10 soil samples (6.2 cm diameter, 30 cm depth) were collected at 2 m intervals along transects in each vegetation type and exclosure, and along paired transects 5–10 m outside exclosures. Samples were analyzed by methods in USDA Natural Resources Conservation Service (1996) for N and C content.

Root samples in 4-year exclosures were collected in the fall of 1996 and the fall of 1998 in 35-year exclosures. We removed three root cores (6.35 cm in diameter, 20 cm deep each) from ungrazed and grazed plots for each vegetation type at the 35-year and 4-year exclosures. Cores were washed to remove soil, oven-dried, brushed to remove large particles of soil, sorted to coarse (>2 mm) and fine (<2 mm) components, and analyzed for biomass differences and N content. A subsample of roots was weighed, combusted at 550°C for 6 hours, then weighed to determine percent organic matter based on the ash sample. Actual root biomass was determined by multiplying % organic matter by the weight of the entire dried root sample.

Nitrogen Fluxes

N Inputs and Transfers

Litterfall was collected as part of a companion study (Menezes et al. 2001) at 4-year exclosure sites during the falls of 1995, 1996, and 1997, and at 35-year sites during the fall of 2000 in upland grass/shrub and aspen vegetation types (Table 1). Litter was collected using

plastic greenhouse trays (15 trays, 2.3m² total area 4-yr and 20 trays, 3.1m² total area in 35-yr) placed in grids or linear transects in both ungrazed and grazed treatments at each site. In upland grass/shrub, we alternated the position of trays under and between shrubs. Litter was collected weekly to bi-weekly from September to October until litterfall was complete. The litter was then composited within each experimental replication, sorted by litter type, dried, and weighed. Litterfall biomass was calculated as oven dry mass per unit area. Total N and C content of litter was determined using a LECO CHN-1000 analyzer.

We measured elk fecal and urinary deposition from plots to determine the amount of N input by elk. We established three line transects in each of the main valleys, and placed eight 1-m² randomly located plots along each transect (9 transects, 72 plots total). Transects were sampled in the winters of 1997–1998 and 1998–1999. Plots were cleared and new fecal piles/plot recorded at the end of each season. We collected 22 piles of fresh elk feces to determine average N content/pile and average mass/pile. Samples were oven dried, and N and C content/pile determined using a LECO CHN analyzer. Fecal N added to sites during winter was calculated by multiplying fecal mass by % N of feces.

We estimated urinary input from elk with a ratio of urinary N to fecal N (U_{ratio}) using the formula: $U_{ratio} = 2.66-1.1DN$, derived from studies by Mould and Robbins (1981) assuming an average mass of elk of 200 kg, where DN = digestible N. Total input from urine and feces was calculated from: $N_{total} = FN + U_{ratio}FN$, where FN = fecal N. Estimates for volatilization loss from urine patches were taken from Schimel et al. (1986) and Jarvis et al. (1989).

To determine potential rates of transfer by elk between different vegetation types, (e.g., between willow, aspen, mixed conifer, mesic meadow, upland grass/shrub, and Ponderosa pine/shrub), we observed groups of radio-collared elk for 24-hour periods, one to two times per month during the winters of 1997–1998 and 1998–1999. We recorded behavior, location, vegetation type, group size, and movements of one to five groups for 24-hour periods. We pooled locations by time of day: morning (0600–0959 hr), midday (1000–1559 hr), evening (1600–1759 hr), and night (1800–0559 hr).

To estimate N transferred by elk during seasonal migrations, we calculated elk body mass losses and gains on summer and winter ranges using data from Cassier (1990) and Murie (1951). We followed Hobbs et al. (1982) for converting body mass lost to N and used population estimates from Lubow et al. (this volume).

Decomposition, Mineralization, and Soil N Availability

Decomposition was sampled as part of a companion study (Menezes et al. 2001). Net N mineralization was estimated with the closed top-core technique (Adams and Attiwill 1986). Plastic tubes were pounded 15 cm into the mineral soil and capped for incubation periods ranging from 4 weeks (summer) to 6 weeks (autumn) to 6 months (winter). After the incubation period, soils were collected, mixed, and 10-g subsamples extracted for 24 hours with 100 mL of 2 M KCl. Ammonium-N and nitrate-N were determined with Perstorp automated colorimetry. Net N mineralization was calculated as the post-incubation concentrations of ammonium and nitrate minus the concentrations from paired cores taken at the beginning of each incubation period. About half of the net mineralization rates were negative, so these values were set to 0 (representing no N available to plants for that sample location and period). The net N mineralization rates were summed across periods to give an annual estimate.

Soil N availability was assessed using ion-exchange resin bags (Binkley and Hart 1989) in 1995, 1996, and 1998 in 4-year exclosures (Menezes et al. 2001). Resin bags were also used at 35-year exclosures to estimate availability of ammonium-N and nitrate-N. In each vegetation type, 10 bags were placed 2 cm below the mineral soil surface, at 2 m intervals along a transect from May 1998 to October 1998, and again from October 1998 to May 1999. The two-section (anion and cation) resin pouches were combined and extracted with 100 mL of 2M KCl. Concentrations of ammonium and nitrate were determined colorimetrically on a Perstorp autoanalyzer.

Elk Consumption

To measure winter herbaceous consumption by elk, six 1-m² grazing cages were randomly located at grazed plots of 4- and 35-year exclosures. Paired 0.25m² quadrats inside and outside cages were clipped in spring prior to greenup. Cages were randomly replaced after spring sampling to measure early summer consumption that occurs while elk migrate to summer ranges. Clipped vegetation was dried at 55°C in a forced air oven for 48 hours, and then weighed. Percent consumption was determined by the difference method:

$$\% \text{ consumption} = 100 \times (B_i - B_o)/B_i$$

where B_i = dry weight of biomass inside grazing cage, and B_o = dry weight of biomass outside cage.

Statistical Analysis

Non-normal data was transformed using arcsine square root transformations and SAS statistical software. Satterthwaite's t-test for unequal variances was conducted, unless otherwise noted. The F-protected least significant difference was used to determine significant differences between grazing treatment means in willow sites. Differences were determined at the 90% level ($P \leq 0.10$).

Biogeochemical Modeling

We simulated long-term responses of soil C, N, net N mineralization, total shrub C, shrub C production, shrub coarse root C, shrub fine root C, and aboveground live grass C using the CENTURY model (U.S. National Science Foundation Ecosystem Studies Research Project 1983). CENTURY simulates the long-term dynamics of C, N, P, and sulfur (S) for grassland, crop, forest, and savanna systems. The soil organic (NELEM) submodel simulates the flow of C and N through plant litter and the inorganic and organic pools in the soil. We entered major input variables using our empirical data whenever possible including: (a) monthly average maximum and minimum air temperatures (from Estes Park weather station); (b) monthly precipitation (from Estes Park weather station); (c) lignin content of plant material (this study); (d) plant, N, P, and S content (this study); (e) soil texture (R. Menezes, unpublished data); (f) atmospheric N inputs (from Baron et al. 2000); (g) N recycling from elk (this study); (h) initial soil C and N levels (this study); and (i) N and C removals by elk (this study). The model includes three soil organic matter pools (active, slow, passive) with different potential decomposition rates, above and belowground litter pools, and a surface decomposing litter pool. Decomposition rate is a function of precipitation, monthly temperature, and monthly potential evapotranspiration. The N associated with C lost in respiration was assumed to be mineralized. For total litter inputs with C:N ratios similar to this study, the model assumes decomposition results in net N mineralization, and decomposition of the structural component of the litter results in N immobilization (Parton et al. 1987; Metherell et al. 1993).

We simulated three scenarios of elk density and elk offtake: (a) no change from current density or offtake levels; (b) a 25% increase over current offtake levels on willow to simulate a possible further increase in elk numbers in the entire town-park population, increased willow use as elk numbers increase, and/or invasion of the winter range by moose (*Alces alces*) that currently inhabit the west side of the park (moose prefer willow as a key forage and even a few moose that enter the area would raise herbivory levels on the willow); and (c) a 40% less offtake by elk to simulate suspected offtake in the absence of human-altered forages in town, and if wolves (*Canis lupus*) and brown bears (*Ursus arctos*) were still present (Singer et al. 2002). The model was run for the previous 10 years to equalize the model and then 50 and 100 years into the future. We simulated only the upland grass/shrub and the willow vegetation types where our empirical data were most complete. We calculated weighted means for vegetation input variables to the CENTURY model by multiplying grams of biomass in the system by proportion of total biomass for the two vegetation types modeled.

Results

Nitrogen Pools

Aboveground N Pools

Elk herbivory reduced the structure (height, canopy volume, stem density) of willows and CAG produced by willows by 66% after 4 years ($P = 0.05$) and 98% after 35 years ($P = 0.10$) compared to protected willows (Table 2). Elk herbivory also reduced herbaceous production in the willow type by 22% after 4 years, but this difference was not significant (Table 2). Elk herbivory similarly reduced mean height and annual biomass production of several shrubs in the upland grass/shrub type (67% reduction in CAG after 35 years; $P = 0.01$). Annual herbaceous biomass produced in upland grass/shrub was not substantially altered by ungulate herbivory after 4 years, but decreased 32% after 35 years ($P = 0.10$) of protection. This was most likely due to the large increase in shrub cover of *A. tridentata* after 35 years of protection.

Concentrations of N were not greatly altered by elk herbivory (Table 2). We found increased N concentrations in only 4 of 13 grazed plant species (*A. tridentata*, $P = 0.10$; *Bouteloua gracilis*, $P = 0.01$; *Heracleum sphondylium*, $P = 0.09$; and *Koeleria macrantha*, $P = 0.01$) after 35 years of treatment. Higher N concentrations were also found in grazed forb species in the willow type after 35 years ($P = 0.01$), and in grazed upland shrubs after 35 years ($P = 0.02$; Table 2).

Elk herbivory reduced annual N yield (N produced/m^2/yr) of willows by 64% after 4 years ($P = 0.05$) and 98% after 35 years ($P = 0.10$), and N yield of upland

Table 2. Mean production and nitrogen values (and standard errors) of vegetation grazed by elk and protected from grazing for 4 years and 35 years. Root values are in grams/m^2 at 0–20 cm soil depth. * indicates significant difference (P <0.10).

	Production (g/m²/yr)				Nitrogen concentration (%)				Nitrogen yield (g/m²/yr)			
	4-yr treatment		35-yr treatment		4-yr treatment		35-yr treatment		4-yr treatment		35-yr treatment	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Willow (tall and short pooled)												
Total herbaceous (g/m²)	496±90	385±52	391±41	415±91	1.78±0.15	2.00±0.19	1.50±0.14	1.64±0.17	9.09±2.35	7.40±0.92	6.09±0.64	6.78±1.48
Forb (g/m²)	101±29	69±22	78±18	22+14*	2.43±0.22	2.50±0.22	2.31±0.07	2.62±0.06*	2.81±0.72	2.13±0.53	1.79±0.40	0.58±0.35*
Graminoid(g/m²)	406±78	319±45	299±52	393+144	1.72±0.18	1.88±0.21	1.34±.10	1.42±0.11	7.31±2.04	5.93±1.02	4.07±0.83	5.76±2.09
Shrub (g/m²)	82±22	28±8*	229±103	5.0±1.4*	1.71±0.07	1.71±0.05	1.63±0.05	1.82±0.08	1.32±0.31	0.48±0.14*	3.74±1.68	0.09±0.03*
Coarse roots (g/m³)	1,168±470	414±125	44±3	160±24*	0.64±0.11	0.73±0.10	0.69±0.17	1.10±0.48	7.74±3.21	2.60±0.57	0.31±0.09	1.98±1.14
Fine roots (g/m³)	2033±384	3,055±1206	857±61	2,676±714*	0.97±0.06	0.93±0.11	0.72±0.04	1.09±0.01*	20.6±4.81	37.2±21.9	6.19±0.60	29.2±7.87*
Litterfall (g/m²)	65±11	33±8*	-	-	1.25±0.1	1.49±0.1*	-	-	0.57	0.24	-	-
Upland grass/shrub												
Total herbaceous (g/m²)	193±55	111±4	48±8	71±2*	1.22±0.10	1.38±0.07	1.11±0.01	1.22±0.06	2.36±0.72	1.53±0.09	0.54±0.09	0.87±0.02*
Forb (g/m²)	101±55	42±15	12±3	14±6	1.47±0.17	1.69±0.20	1.47±0.17	1.69±0.20	1.56±0.94	0.72±0.23	0.18±0.04	0.24±0.09
Graminoid (g/m²)	92±39	69±13	36±13	58±2	0.97±0.14	1.21±0.05	1.11±0.01	1.22±0.06	0.89±0.41	0.82±0.14	0.40±0.15	0.70±0.01
Shrub (g/m²)	18±9	16±7	159±2	53±15*	-	1.19±0.1[a]	1.24±0.04	1.58±0.13*	-	0.20±0.04	1.98±0.08	0.59±0.05*
Coarse roots (g/m³)	10±5	95±29*	53±21	69±55	0.59±0.09[b]	0.87±0.13	0.59±0.09	1.59±0.99	0.06±0.03	0.83±0.25*	0.30±0.07	1.65±1.56
Fine roots (g/m³)	364±99	345±101	208±56	162±5	0.85±0.17	1.07±0.21	0.76±0.03	0.79±0.11	2.14±0.58	3.00±0.88	1.62±0.51	1.27±0.15
Litterfall (g/m²)	-	-	8±2	12±3	-	-	0.74±0.06	0.74±0.07	-	-	0.05±0.02	0.10±0.01
Aspen												
Total herbaceous (g/m²)	-	-	123±20	121±37	-	-	1.90±0.12	1.68±0.07	-	-	2.37±0.52	2.06±0.71
Forb (g/m²)	-	-	43±11	36±16	-	-	2.99±0.03	2.82±0.14	-	-	1.29±0.32	1.05±0.49
Graminoid (g/m²)	-	-	80±9	85±21	-	-	1.35±0.09	1.15±0.12	-	-	1.09±0.18	0.94±0.14
Shrub (g/m²)	-	-	-	-	-	-	-	-	-	-	-	-
Coarse roots (g/m³)	-	-	418±248	310±232	-	-	0.91±0.37	0.94±0.32	-	-	2.83±0.65	4.19±3.71
Fine roots (g/m³)	-	-	358±53	406±202	-	-	1.18±0.22	1.03±0.04	-	-	4.16±0.22	3.70±1.37
Litterfall (g/m²)	-	-	203±22	36±8*	-	-	0.70±0.01	0.50±0.01*	-	-	1.42±0.49	0.19±0.11

[a]Value from Hobbs et al. (1981).

[b]Value from 35 year data, since no coarse roots available during sampling year for nutrients. Production numbers for these coarse roots were derived from averaging 1995 and 1996 estimates.

shrubs by 70% ($P < 0.0001$; Table 2). Nitrogen yield of herbaceous vegetation in upland grass/shrub type was reduced after 35 years of protection from grazing ($P = 0.07$; Table 2).

Belowground N Pools

We found no effect of grazing treatment on soil N concentration in either 4- or 35-year exclosures, with the exception of a single sample site at mid-slope aspen type at 35-year exclosure 2, which had significantly higher N in grazed than ungrazed plots at depths of 0–15 cm and 0–30 cm ($P <0.10$).

After 35 years of treatment in willow type, we found differences in fine root biomass ($P = 0.0009$), fine root N concentration ($P = 0.003$) and N yield ($P = 0.10$), but not in upland grass/shrub communities (Table 2). Coarse root biomass was nearly four times greater in grazed than ungrazed sites ($P = 0.03$; Table 2). Coarse root production was higher in grazed plots of upland grass/shrub communities ($P = 0.02$) after 4 years, but no differences were found in 35-year treatments (Table 2).

Nitrogen Fluxes

N Inputs and Transfers

Elk herbivory greatly reduced the sizes (height, diameter, volume) of some shrubs (*Salix* spp., *A. tridentata*) and thus reduced the amount of shrub leaf litterfall. After 4 years, biomass of litterfall in willow type was significantly higher in ungrazed than grazed plots ($P <0.05$; data combined for 1995, 1996, and 1997; Table 2). No significant grazing treatment differences were detected for herb or wood litterfall in willow sites. Willow leaf litter N content was significantly higher in grazed than ungrazed plots ($P <0.05$). At 35-year treatments, aspen litterfall biomass was four times higher in ungrazed than grazed plots ($P <0.0001$; Table 2). At ungrazed sites in upland grass/shrub communities, litter biomass was higher specifically in leaf ($P = 0.005$), and wood ($P = 0.04$) litterfall, but not for overall litter biomass. Litterfall N content was higher in ungrazed than grazed plots in aspen type ($P <0.0001$), but no difference in N concentration was found in upland grass/shrub litter (Table 2).

Elk deposited substantial amounts of fecal and urinary N on the winter range (Fig. 2). Fecal-N deposited averaged 0.71 g/m²/yr in grazed sites in all the valleys (Table 3). The highest deposition was at Moraine Park ($P = 0.115$) compared to Horseshoe Park and Beaver

Meadows. Nitrogen concentration was 1.53% of fecal pile mass and the average mass was 138 g/pile (n = 22 piles); thus average N content/pile was 2.1 g N. The highest amount of fecal-N deposited was in willow vegetation (Table 3). We calculated an urinary-N:fecal-N ratio of 0.9768 and thus estimated the average urinary-N input from elk was 0.69 g/m²/yr. We estimated the total combined N input from both fecal- and urinary-N as 1.41 g/m²/yr in grazed sites (Table 3) versus 0 g/m²/yr in ungrazed sites.

During eleven 24-hour observation periods, elk were observed 49% of the time bedded and 51% grazing. They were observed more often grazing in morning and evening ($P = 0.0001$), and more often bedded at night ($P = 0.0001$) than other times of the day (Table 4). Overall, elk were observed more often in mesic meadow vegetation (58%; $P = 0.0005$) than all other vegetation types, including Ponderosa pine/shrub (16%), upland grass/shrub vegetation (10%), willow (7%), mixed conifer (7%), and aspen (2%). There were no differences in use of vegetation types in the morning, but elk were observed significantly more in mesic meadow vegetation in midday and evenings ($P <0.05$; Table 5). Elk were seen in mixed conifer and mesic meadow vegetation at night, and mesic meadow, aspen, willow, and upland grass/shrub vegetation in the evenings between 4 and 6 p.m. Elk appeared to be grazing in all vegetation types in mornings, in primarily mesic meadow during midday and evenings, and in willow, mixed conifer, and mesic meadow vegetation types at night. Elk transported N from the aspen, mesic meadow, and willow types where they spent more time feeding, to the conifer types where they spent less time feeding. The net movement of N away from aspen type was 0.60 g N/m²/yr (1.13 g N/m²/yr removed by elk grazing minus 0.53 added by feces and urine; Table 6). Similarly, the net movement of N away from the willow vegetation type was 2.01 g N/m²/yr (4.23 g N/m²/yr removed by elk minus 2.22 g N/m²/yr added by feces and urine; Fig. 2). Seasonal estimates of elk body mass gained on the summer range and lost on the winter range suggest a net transfer by elk of 0.016 g N/m²/yr from summer to winter range.

Decomposition, Mineralization, and Soil N Availability

We documented lower N mineralization in grazed versus ungrazed plots of short willow sites after 4 years of protection (0.39 grazed versus 1.83 ungrazed, $P = 0.07$, n = 4 sites, versus 3.25 grazed and 2.11 ungrazed, $P > 0.10$, n = 4, in tall willow sites). Nitrate pools were also lower in grazed than ungrazed plots of short willow
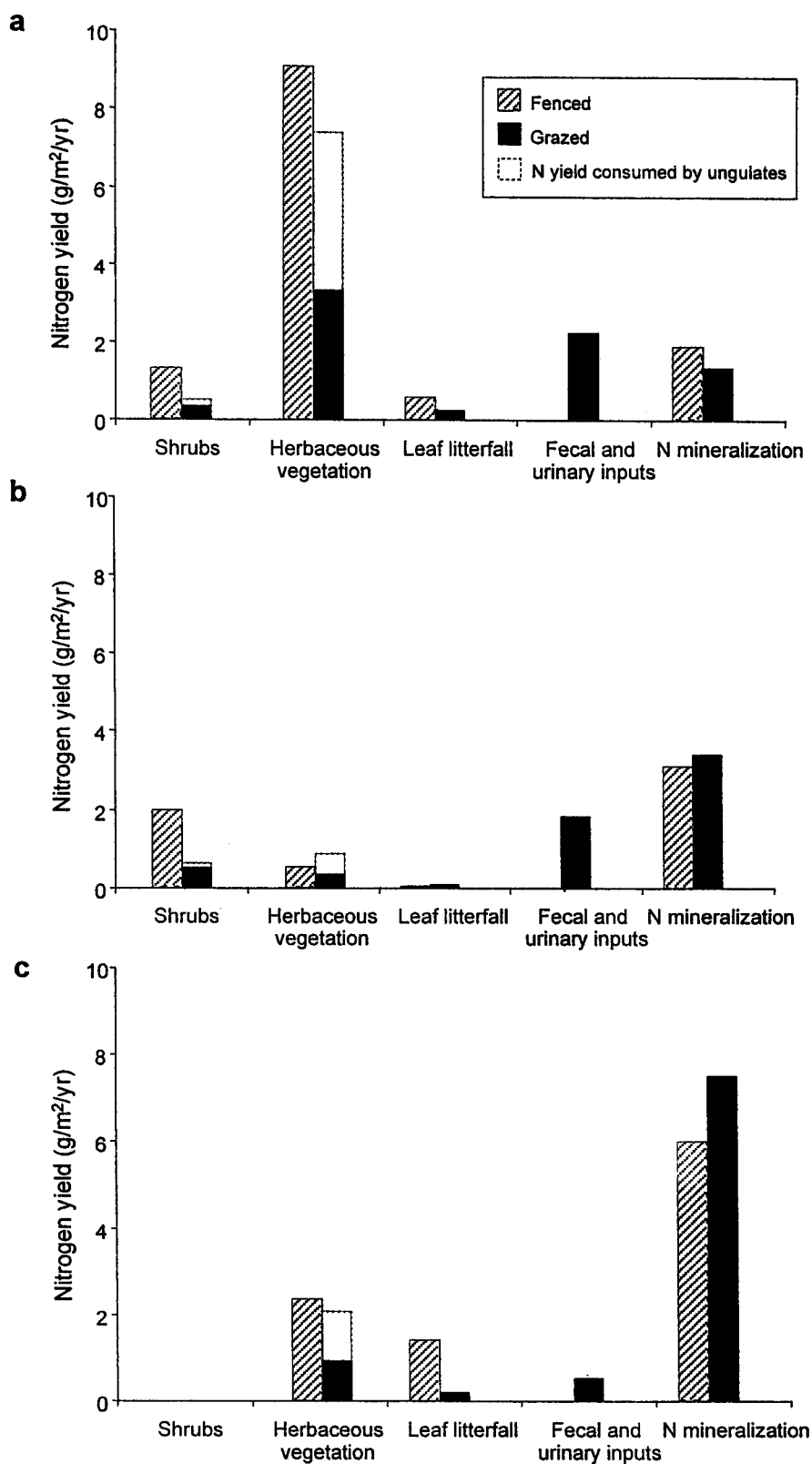
Fig. 2. Annual nitrogen produced by vegetation, removed by elk herbivory, fecal/urinary inputs by elk, and mineralization rates on the elk winter range, Rocky Mountain National Park, Colorado, in (a) tall and short willows pooled (4-year treatment data); (b) upland grass/shrub (35-year data), and (c) aspen (35-year data).

Table 3. Average fecal biomass, fecal-N, urinary-N, and total N deposited in different vegetation types on elk winter range in Rocky Mountain National Park, Colorado, winters 1997–1998 and 1998–1999.

Vegetation type	Number of transects	Average mass deposited (g/m²/yr)	Average fecal-N deposited (g/m²/yr)	Average urinary-N deposited (g/m²/yr)	Average total N deposited (g/m²/yr)
Meadow	10	34.6 ± 15.0	0.53 ± 0.23	0.52 ± 0.22	1.05
Upland grass/shrub	2	60.5 ± 8.6	0.93 ± 0.13	0.90 ± 0.13	1.83
Willow	4	73.4 ± 29.4	1.12 ± 0.45	1.09 ± 0.44	2.22
Aspen	2	17.3	0.26	0.26	0.53
Total average	18	46.44	0.71	0.69	1.41

sites (0.31 grazed versus 1.44 ungrazed, $P = 0.10$), but no differences for these N variables were detected in tall willows. Short willow sites are apparently a browsing induced conversion from the tall willow type (Peinetti et al., this volume), and the two types are structurally and functionally different from each other. Short willow grazed sites had 33% lower herbaceous production, 27% less CAG, and 38% shorter mean willow height than tall willow sites, while tall willow sites had more ground shade.

Elk herbivory had few effects on the structure, function, and N processes in the upland grass/shrub type (Fig. 2). We found no other grazing effect on total soil N availability, with the exception of upland grass/shrub type at 35-year exclosure 1, where NO_3 was three times higher in soil from grazed versus ungrazed plots ($P < 0.10$; n = 1 site). We found no grazing treatment effect on decomposition of willow or sedge litter, but nitrogen losses from litterbags were significantly higher in sedge than willow litter ($P = 0.012$).

Elk Consumption

Annual percent consumption of herbaceous biomass by elk in grazed plots was considerable (Table 6). In short willow sites, herbaceous consumption by elk averaged 67 ± 11% and 41 ± 7% in tall willow sites. Shrub CAG consumption (primarily bitterbrush) averaged 12 ± 3% in upland grass/shrub, and 33 ± 2% in pooled willow vegetation types during winter.

Biogeochemical Modeling

Upland Grass/Shrub

If elk herbivory was reduced 40% relative to current levels, CENTURY predicted elk grazing was sustainable. Total soil C, total soil N, net N mineralized, total shrub C, and coarse and fine root C would be roughly stable over periods of 50 and 100 years into the future. However, current levels of consumption by elk might decrease nutrients slightly. CENTURY predicted

Table 4. Average percent of time elk were observed bedded or grazing at different times of day during eleven 24-hour observation periods on the elk winter range, Rocky Mountain National Park, Colorado, winter of 1997–1998 and 1998–1999 (± SE).

Time of day	n	Average % of time bedded	Average % of time grazing
Morning	40	21 ± 5	79 ± 5
Midday	68	54 ± 4	46 ± 4
Evening	26	10 ± 2	90 ± 2
Night	123	63 ± 3	37 ± 3

Table 5. Average percent of time at different times of day that elk were observed in each vegetation type during eleven 24-hour observation periods on the elk winter range, Rocky Mountain National Park, Colorado, winters 1997–1998 and 1998–1999 ($\pm$ SE).

Time of day	Mesic meadow	Upland grass/shrub	Willow	Aspen	Mixed conifer	Ponderosa pine/shrub
Morning	23 ± 4	12 ± 3	18 ± 4	14 ± 4	17 ± 5	16 ± 6
Midday	35 ± 4	11 ± 2[a]	9 ± 2[a]	9 ± 3[a]	20 ± 5[a]	16 ± 3[a]
Evening	36 ± 4	22 ± 4[a]	16 ± 2[a]	11[a]	No observation	15 ± 2[a]
Night	26 ± 4	11 ± 4[a]	15 ± 6	6 ± 3[a]	28 ± 17	14 ± 4[a]

[a]Denotes significant difference ($P \leq 0.05$) to mesic meadow vegetation type, the most used type.

total soil C would decrease 2% in 50 years, and 2.5% in 100 years, total soil N would decrease 0.5% in 50 years and 1% in 100 years, net N mineralized would decrease 0.7% in 50 years and 1.5% in 100 years, total shrub C (below and aboveground) would decrease 4% in 50 years and 7% in 100 years, and aboveground live grass C would decrease 0.4% in 50 years and 0.7% by 100 years (Fig. 3).

If levels of consumption increased 25% due to elk population increases and/or moose expansion into the area, larger nutrient losses were projected. Soil C would decrease 4% in 50 years and 5% in 100 years; total soil N would decrease 1% in 50 years and 2% in 100 years; net N mineralized would decrease 2% in 50 years and 3.5% in 100 years, while aboveground live grass C would increase 0.01% in 50 years (Fig. 3). The largest projected declines were in total shrub C, which decreased 15% in 50 years and 26% in 100 years. These projected nutrient declines were due to both consumption of vegetation by elk and to the secondary effects of elk herbivory, such as large reductions in sizes of several shrub species and the subsequent reduction in high quality and decomposable shrub leaf litter.

Willow

The model projected slightly larger decreases in C and N in willow vegetation type at current and higher elk consumption scenarios than for the upland grass/shrub type, except for total shrub C (Fig. 3). These larger predicted decreases were due to a combination of higher offtake levels by elk in willow vegetation and the reduction in sizes of shrubs (willow and birch) and

subsequent lower shrub leaf litter inputs. Movement of N away from vegetation types where preferential feeding by elk occurred (aspen, willow) also contributed to a loss of nitrogen.

Discussion

Elk herbivory had a potentially large negative effect on N and C dynamics in willow and aspen types. We concluded elk herbivory and activity resulted in a net transfer and loss of N from these vegetation types. Elk reductions in willow shrub size, aboveground N pools, shrub litter, willow annual N yield, and elk consumption was not compensated for by elk inputs of fecal and urinary N [and N mineralization and N pools (NO_3) were lower after 4 years in short willow sites]. Elk consumption was also not compensated for by elk inputs in the aspen type. Long-term projections from the CENTURY model tended to support these conclusions. Nevertheless, we concluded that elk herbivory and activity resulted in almost no net change in N in the upland grass/shrub type. Elk apparently returned approximately as much N to the system to compensate for N removals from grazing and changes to N yield due to reductions in canopy size of shrubs. Long-term projections from the CENTURY model also tended to support this conclusion. The model projected only a 0.5% decline in soil N in 50 years at current high elk densities – a decline that would likely be difficult to detect using standard sampling techniques. More time may be needed to detect any additional changes, especially any effects on slower changing N pools.

Table 6. Estimated nitrogen inputs and outputs based on herbaceous offtake in four vegetation types on elk winter range, Rocky Mountain National Park, Colorado, 1998–1999.

Vegetation type	% of elk group observed feeding	% of time in vegetation type	N added by elk $(g/m^2/yr)$[a]	% herbaceous/ shrub offtake	N removed by elk based on % offtake $(g/m^2/yr)$	Net gain or loss of N due solely to elk inputs (feces, urine) and offtake $(g/m^2/yr)$	CENTURY modeled effects on soil N $(g/m^2/yr)$[b]
Aspen	92	7	0.53	55[c]	1.13[c]	-0.60	n.d.
Mesic meadow	51	39	1.05	56/NA	2.69	-1.64	n.d.
Upland grass/shrub	65	17	1.83	60/12	0.59	+1.24	-0.03
Willow	74	13	2.22	55/33	4.23	-2.01	-0.08

[a]Based on fecal plots sampled 1997–1999.

[b]Annual effects on soil N due to all effects of elk inlcuding secondary effects on plant morphology.

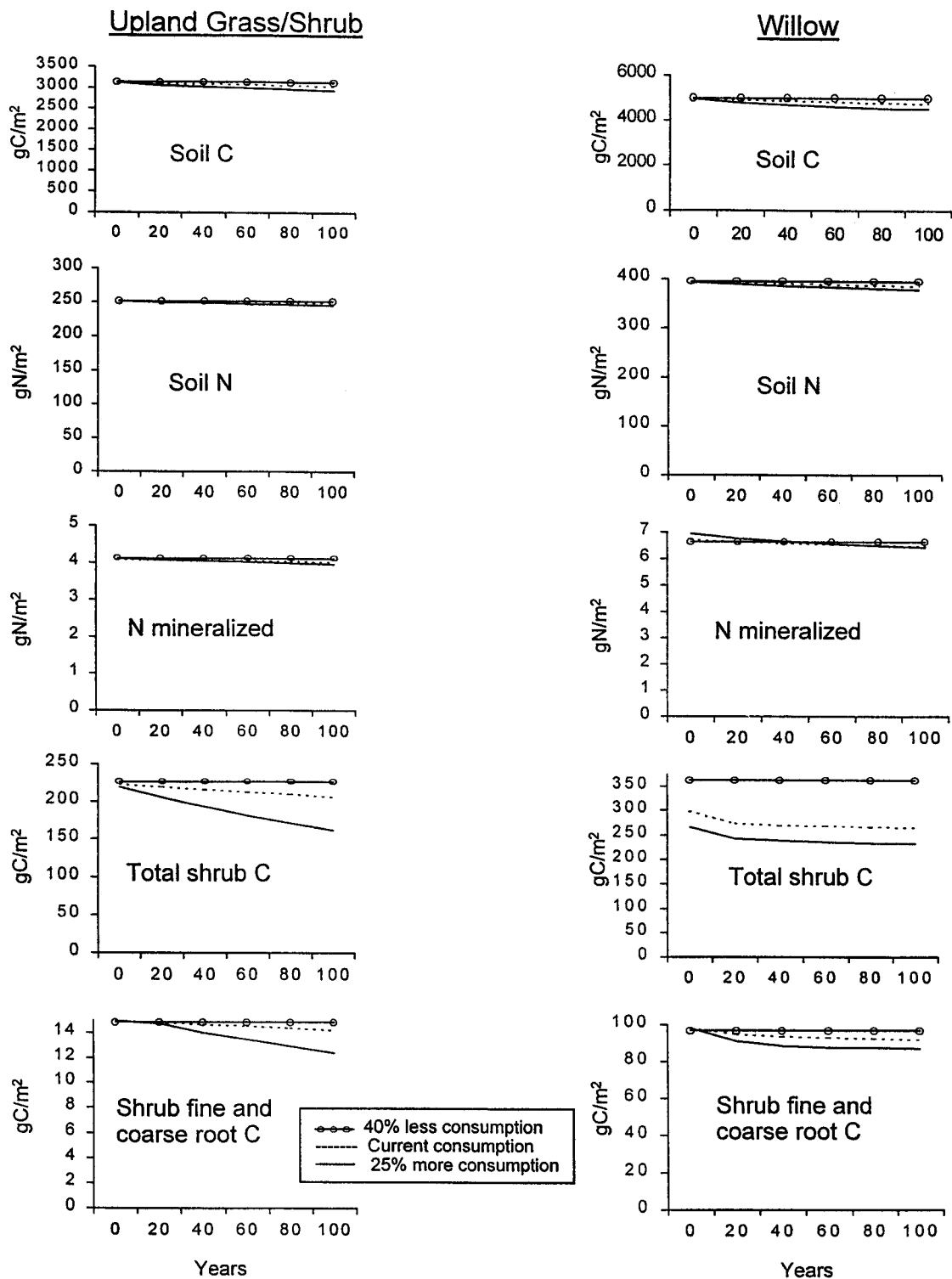[c]Winter offtake only; no summer or shrub data available.

NA = not applicable.

Fig. 3. Results of CENTURY model simulations on carbon and nitrogen in upland grass/shrub and willow vegetation types predicting effects of elk grazing up to 100 years into the future under different consumption levels in Rocky Mountain National Park, Colorado.

In contrast to our findings of lower N mineralization and N pools in the short willow type, other authors have reported increases in N mineralization due to grazing (Ruess 1984; Ruess and McNaughton 1987) and increases in the rate of N recycling as a result of fecal and urinary deposition. Soil mineral N levels were highest at moderate grazing levels in grasslands, but other model efforts have suggested overgrazing would deplete N. As in our study, Seagle et al. (1992) found a decrease in net soil N mineralization with heavy grazing. There is evidence that elk herbivory may be high enough in the short willow type to reduce N processes.

We found higher N concentrations in only one-third of the grazed plant species we sampled and in willow litter on grazed sites. This is consistent with many studies, which report higher N concentrations in plant tissues due to native ungulate herbivory (McNaughton 1984; Coughenour 1991; Singer 1995; Singer and Harter 1996). Typically, higher N concentration in grazed plants is associated with higher N mineralization on grazed sites (Frank and Groffman 1998; Ritchie et al. 1998). We do not know why mineralization rates were not higher due to grazing in RMNP grasslands. Our findings generally fit the criteria for decelerated N cycling predicted by Ritchie et al. (1998), at least in short willow sites.

We caution that we did not sample or quantify the entire N cycle in this ecosystem and that several unknowns exist. For example, volatilization from urine was not measured, but other research suggests these losses would be minor [10–15% of urinary N; Vallis et al. (1982); Schimel et al. (1986)]. In either case, the losses of N from urine might be less than the volatile losses from ungrazed plants, and thus ungulates might even reduce total volatile losses of N (Ruess and McNaughton 1987; Detling 1988). No effects of elk on leaching of N from soil were reported by a companion study (Binkley et al., this volume). Water erosion losses were unknown.

We concluded elk were transferring N between vegetation types and winter and summer ranges. In agreement with Frank et al. (1994) for Yellowstone National Park, our calculations for body mass lost on the winter range combined with winter elk consumption measurements, suggest there is a net movement of N over the year from summer to winter range by elk. Elk appeared to be preferentially feeding in aspen type in RMNP, as opposed to other types, and were transporting N away from aspen to surrounding vegetation types. In addition, our aspen offtake rates are for winter only, suggesting that elk may be having an even greater effect than we report here, if we were able to include summer offtake

as well. Aspen type comprises a small part of the elk winter range (2%), thus elk may be having a significant effect in this type but relatively less impact on N dynamics across the entire winter range. McNaughton (1993) reported that African ungulates seek shade when they rest and deposit more feces and urine under trees than in the open. A redistribution of N means bedding areas in conifer forests might be enriched, while willow and aspen types would be depleted. At some point, the depletion might result in the slowing of plant growth rates and changes in plant species composition (McInnes et al. 1992; Ritchie et al. 1998).

Management Implications

Our findings concerning the effect of elk herbivory on nitrogen cycling and plant growth responses were somewhat conflicting. On one hand we documented substantial declines due to elk in the amount of N deposited to the soil in both willow and aspen vegetation types, but on the other hand we documented little effect of elk in the upland grass/shrub type. Observational studies of elk verified that elk were transporting N from willow and aspen types, their preferred feeding types, primarily to the conifer types, their favored bedding habitat. We predict declines in N in the willow and aspen types, a prediction also generally supported by CENTURY soil modeling, although the CENTURY model predicted smaller declines.

In support of these predictions, we found a decline in the NO_3 pool and N mineralization due to elk herbivory in the short willow type, but not in the upland grass/shrub type. Perhaps not enough time has passed to document other altered N pools or N mineralization rates. Therefore, we recommend conservative management of elk numbers and grazing effects, since: (1) all modeling scenarios of increased elk density resulted in projections of decreases in N and C; (2) scenarios of reduced elk density were more optimistic; and (3) a decline in N processes was found in one vegetation type. Conservative management of elk numbers would be appropriate until more time has passed to study the slow changing N pools and until further research is conducted on the effects on plant communities of observed differences in N processes and pools.

Acknowledgments

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